Jl S. Afr. Bot. 46 (3): 233–243 (1980)

GERMINATION AND SEEDLING MORPHOLOGY OF *JUBAEOPSIS CAFFRA* BECC. (PALMAE)

B. L. Robertson

(Department of Botany, University of Port Elizabeth)

Abstract

Germination, which is remote-tubular, involves five steps. Firstly, the radicle appears through the germination pore in the endocarp. In stage two, lasting 10–12 days, the apocole grows downwards to an ultimate depth of 70 mm. Twenty days later, the apocole swells distally as the plumule enlarges in step three. Characteristic of stage four is the longitudinal splitting of the cotyledonary sheath followed by the emergence of the first scale leaf 43 days after stage one. A second scale leaf appears 12 days later. Three negatively geotropic lateral roots develop from the primary root. The appearance of the first eophyll, 80 days after the onset of germination represents the fifth step.

Growth of the seedling is slow and only seven foliage leaves are produced in the first 570 days. The first six are entire, lanceolate leaves while the seventh is initially bifid but later becomes irregularly pinnate with reduplicate pinnae to form the first typical compound leaf.

Uittreksel

ONTKIEMING EN SAAILING MORFOLOGIE VAN *JUBAEOPSIS CAFFRA* BECC. (PALMAE)

Ontkieming, wat verwyderd-buisagtig is, behels vyf stappe. Eerstens verskyn die radikula deur die kiemingsporie in die endokarp. In stap twee, wat 10–12 dae duur, groei die saadlobbuis afwaarts tot 'n maksimum diepte van 70 mm. Twintig dae later swel die distale gedeelte van die saadlobbuis namate die plumula vergroot. Kenmerkend van stap vier is die lengtespleet wat in die saadlobskede ontstaan namate die eerste skubblaar verskyn. 'n Tweede skubblaar volg na 'n verdere 12 dae. Drie negatief-geotropiese sywortels ontwikkel vanuit die primêre wortel. Die verskyning van die eerste loofblaar, 80 dae na die aanvang van kieming verteenwoordig stap vyf.

Groei van die saailing is stadig en slegs sewe loofblare word in die eerste 570 dae gevorm. Die eerste ses hiervan is gaafrandige, lineêre gelanseoleerde blare terwyl die sewende blaar aanvanklik tweespletig is, maar verander later na onreëlmatig geveerd met terugverdubbelde pinnas om die eerste tipiese saamgestelde blaar te vorm.

Introduction

Germination of palm seeds has been studied for nearly 400 years—the first recorded description being made in 1588 by Camerarius (Gatin, 1906) when he published his findings on the germination of *Phoenix dactylifera* seeds. Subsequent publications on this subject have been numerous but only a few relevant ones will be mentioned here.

In the monocotyledons, where plumular protection is a prerequisite for seedling development, the primary axis, with plumule and radicle is carried out of the

---

Accepted for publication 11th December, 1979.

seed into the soil by the cotyledonary sheath (Burtt, 1972). The extent to which the plant is removed from the seed varies from a few millimetres as in *Archontophoenix* to three metres or more in *Lodoicea* (Tomlinson, 1961).

Using previous systems (Richard, 1811 cited by Boyd, 1932; Martius, 1823–50 cited by Boyd, 1932) Gatin (1906), in a classic study of germination in 33 genera and 58 species of palms, described three basic germination types. The first type, remote-tubular, is exemplified by *Phoenix canariensis*, while the second, adjacent-ligular is found in *Archontophoenix cunninghamiana*. These two types are extremes while the third type, viz. remote-ligular germination, as seen in *Sabal umbraculifera*, is considered as an intermediate type. These three types are apparently comprehensive enough to accommodate all the other palms except possibly the genera *Nypa* and *Phytelephas* (Tomlinson, 1960a).

Germination of palm seeds is almost exclusively hypogeal (Tomlinson, 1960a; 1960b) except in one or two exceptional cases (Moore & Uhl, 1973). The cotyledon never becomes erect or expanded as a green assimilatory blade, but does possess the equivalent of leaf components, viz. lamina, petiole, leaf-sheath and sometimes a ligule (Tomlinson, 1961).

Very little literature is available on the germination of *Jubaeopsis caffra* seeds, and that which has been published is incomplete and, in some cases, questionable. This lack of information can be ascribed mainly to two facts. Firstly, *Jubaeopsis* grows naturally only in two very restricted and remote localities (Wicht, 1967; Robertson & Visagie, 1975) and consequently seeds are not freely available. Secondly, germination of the seeds is slow (up to a year) and the percentage germination is low (Robertson & Small, 1977).

Hill (1937) gives a brief description of *Jubaeopsis*' germination and states that the first leaf breaks through the cotyledonary sheath and expands above the ground. It can be concluded from this that germination is remote but not whether it is tubular or ligular. It would also seem that no scale leaves precede the first eophyll. In the light of Tomlinson's reports (1960a; 1960b) and that by Moore & Uhl (1973) this seems impossible.

Barry (1957) refers to the ". . . vertical descent of the hypocotyl to at least 18 inches below the surface of the soil . . ." in his report on *Jubaeopsis*. It is not clear whether the hypocotyl is borne down to this depth by the apocole or whether the hypocotyl itself elongates. This latter possibility is very unlikely.

Van der Schijff & Snyman (1970) equate the type of germination occurring in *Elephantorrhiza elaphantina* with that of the ". . . South African genera *Phoenix*, *Jubaea* and *Hyphaene* . . .". Apart from the fact that *Jubaea* is not indigenous to South Africa (Corner, 1966), the germination of this monotypic genus is remote-ligular while that of *Phoenix* is remote-tubular. It is not clear whether these authors are in fact referring to *Jubaea* or whether they actually mean *Jubaeopsis*.

The current information on germination of *Jubaeopsis* is thus very sketchy and further, no data concerning seedling morphology and development are available. Consequently, it was deemed appropriate that these aspects be investigated fully.

MATERIAL AND METHODS

Seeds used in this study were obtained from a 43-year-old tree growing in St. George's Park, Port Elizabeth. Germination was hastened by maintaining the seeds at a moisture content of 14 % and incubating them in pure oxygen at 40 °C in the dark (Robertson & Small, 1977). Generally, germination is initiated within 21–30 days under these conditions.

Subsequent to the appearance of the radicle, the seedlings were planted in a mixture of soil, sand and peatmoss in 18 litre plastic containers and placed outside in semi-shade.

RESULTS

(a) *Morphology of seed germination*

Five stages in the germination of *Jubaeopsis* seeds can be recognised.

Stage I: This stage is characterised by the appearance of the radicle and cotyledonary sheath or apocole through one of the three lateral germination pores in the endocarp of the nut. The manner in which the radicle tip emerges from the nut, varies. In some cases the pore lid is ruptured as the embryo breaks through it, while in other instances the intact lid is pushed off.

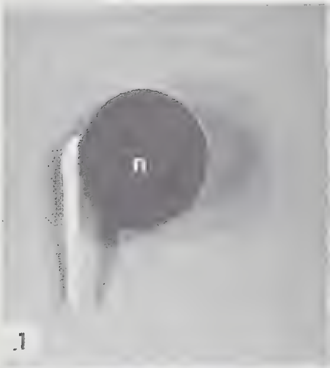
Immediately upon emerging from the nut, the apocole becomes positively geotropic.

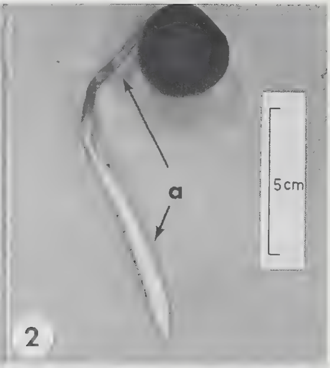
Stage II: In this stage the apocole grows vertically downwards into the soil. The apocole is more or less of uniform thickness over its entire length, but has a sharp distal point (Fig. 1). Growth of the apocole is fairly rapid during this time and within 10–12 days from the onset of germination, reaches a length of approximately 50 mm.

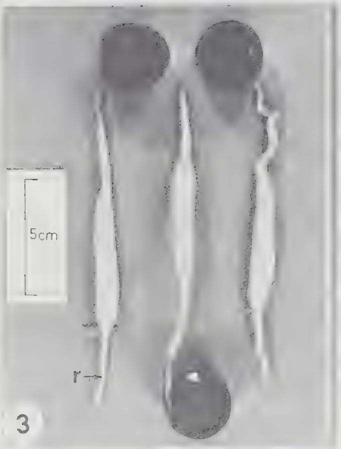
Stage III: Thirty days after the appearance of the radicle from the nut, the distal section of the apocole starts to swell (Fig. 2). This phenomenon characterises Stage III and results from the development of the leaves in the plumule. At this point the apocole and radicle together are 80 to 100 mm long.

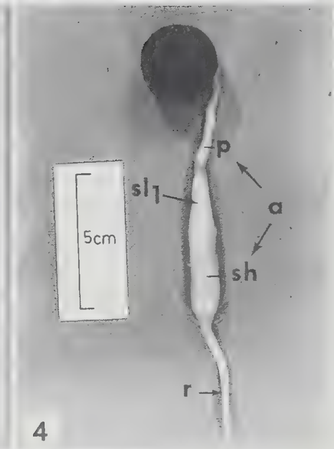
Stage IV: Stage IV is initiated by the longitudinal splitting of the cotyledonary sheath (Figs 3 and 4) as the volume of the plumule increases. Inside the nut the apex of the cotyledon has enlarged considerably during the preceding stages and a haustorium is formed (Fig. 5). This haustorium is the equivalent of a leaf lamina, while the middle piece of the cotyledon, i.e. between the haustorium and the split in the sheath, represents the petiole of a normal leaf. The section of the apocole which has split open, i.e. the cotyledonary sheath, can be equated with the typical leaf sheath found in the normal monocotyledonous leaf (Fig. 4).

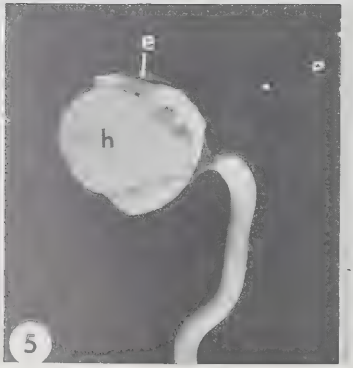
At this time the proximal limit of the primary root is clearly demarcated (Figs 3, 4 and 6). Also characteristic of this stage and following shortly after the


n
1


a
5cm
2


5cm
r
3


p
sl1
a
5cm
sh
r
4


e
h
5

initiation of the split in the cotyledonary sheath, is the development of lateral roots. The first lateral roots, of which there are three, emerge simultaneously and they are spaced evenly around the circumference of the primary root. These are not adventitious roots as they originate distally of the proximal limit of the primary root (Figs 6 and 7).

The first leaf to emerge from the split in the sheath is without a lamina and forms an entire sheath around the younger, developing leaves (Fig. 4). This occurs approximately 43 days after the onset of germination.

Twelve days later the second leaf emerges. This too is a needle-shaped leaf without a lamina and constitutes the second scale leaf (Fig. 7). Both scale leaves are rigid and have no trouble in piercing the soil.

At this stage the primary root is approximately 50 mm long and a number of small lateral roots have developed. These roots are very much smaller than the first three lateral roots which differentiated during Stage III. They are not restricted to any particular region of the primary root, but occur over most of its length and on the first three lateral roots as secondary lateral roots (Figs 6, 7 and 9).

The endosperm in the seed is almost entirely depleted at this stage and the cotyledonary haustorium completely fills the cavity which remains inside the endocarp. The rough nature of the haustorium surface results in the increased effectivity of this organ as an absorptive and digestive structure (Fig. 8).

Stage V: In this stage the first green foliage leaf or eophyll becomes visible (Fig. 9) and it is considered that this stage terminates germination as such and that it represents the first stage in the development of the seedling. This first green, bladed leaf appears 80–90 days after germination is initiated.

FIG. 1.
Stage II in germination of *Jubaeopsis caffra* seeds.

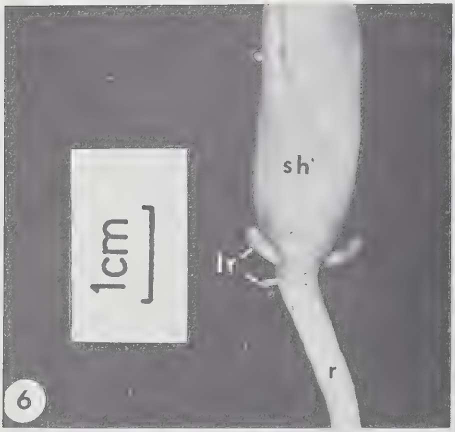
FIG. 2.
Characteristic swelling of apocole in Stage III.

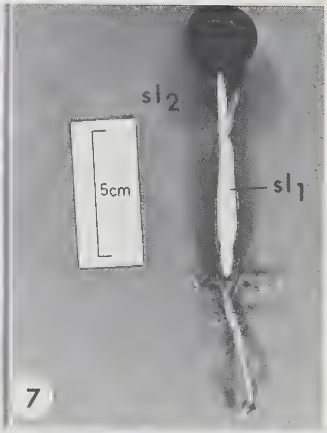
FIG. 3.
Early Stage IV showing the split cotyledonary sheath.

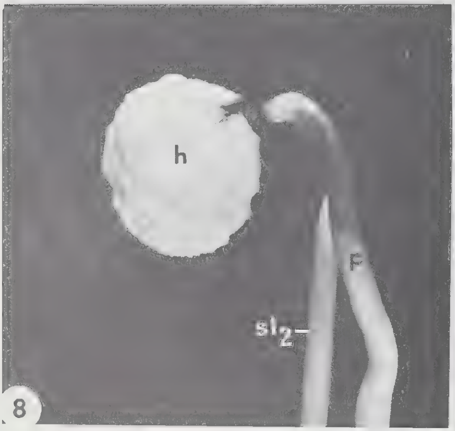
FIG. 4.
Mid Stage IV—first scale leaf emerging.

FIG. 5.
Endosperm and haustorium in Stage III.

(a—apocole; e—endosperm; h—haustorium; n—nut;
p—petiole; r—radicle; sh—sheath; sl_1—first scale leaf).







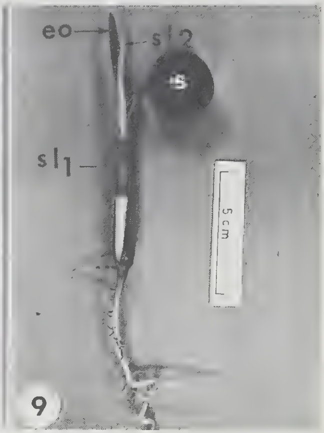


FIG. 6.
Development of first lateral roots during Stage IV.

FIG. 7.
Late Stage IV after emergence of the second scale leaf.

FIG. 8.
Haustorium during Stage IV.

FIG. 9.
Appearance of the first eophyll in Stage V.

(eo—eophyll; h—haustorium; lr—lateral roots; p—petiole; r—radicle; s—seed; sh—sheath; sl_1—first scale leaf; sl_2—second scale leaf)

(b) *Seedling Morphology*

Under experimental conditions, the growth of the *J. caffra* seedling is relatively slow and during the first 570 days of growth only seven eophylls are formed. The actual time of appearance of each of these foliage leaves, is presented in Table 1. No seedlings growing under natural conditions could be studied in this respect and it is thus not known whether the growth of this species is also as slow in its natural habitat as in the experiments.

TABLE 1.
Number of days between germination and the appearance of the first seven eophylls in *J. caffra*.

Eophyll	Days
1	80
2	180
3	280
4	360
5	390
6	540
7	570

The first six eophylls are all entire, linear lanceolate leaves about 400 mm long, the most obvious difference between them being in their width (Figs 10 and 11). The first eophyll attains a width of approximately 30 mm (Fig. 10), while the sixth one is more than 60 mm wide.

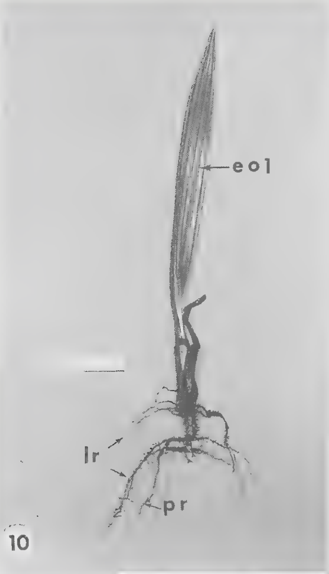
In *J. caffra* the seventh foliage leaf is irregularly pinnate (Fig. 12). The foliage leaves are clearly differentiated into segments which in the first six eophylls are not separated. Arrangement of these segments along the rachis is irregular, especially towards the apex of the leaf.

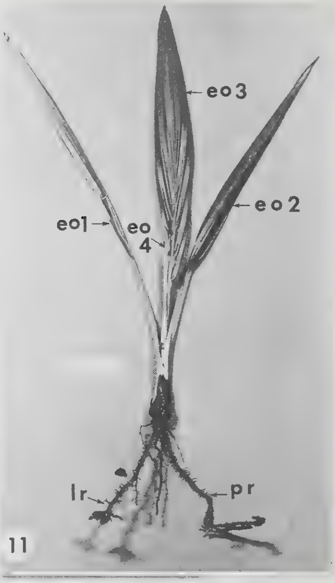
As the seventh foliage leaf appears, its apex is bifid. Subsequent development of this leaf does however result in the segments or leaflets tearing and separating. This separation does not occur in the more apically placed segments and consequently the apex of the seventh eophyll consists of two large, undivided leaflets in contrast to the smaller leaflets lower down on the rachis (Fig. 12).

Root development in the seedling phase is also relatively slow. One year after germination, i.e. at the time when the fourth eophyll becomes externally visible, the primary root is still functional, but it is supported in its activity by the three major lateral roots. These latter roots are nearly as well developed as the main root (Fig. 11).

DISCUSSION AND CONCLUSIONS

In view of the fact that the cotyledon is not extracted completely from the seed and that it does not expand above the ground and function as a photosynthetic


10


11

12

organ, germination of *J. caffra* seeds is hypogeal. This is in accordance with the germination of all other palm species except *Nypa fruticans* (Tomlinson, 1960a, 1960b; Moore and Uhl, 1973).

Further, on the basis of the germination types described and defined by Gatin (1906) the seeds of *J. caffra* exhibit remote-tubular germination.

Apart from distinguishing between the types of germination, Gatin (1906) found that a correlation exists between the type of germination and the structure and orientation of the embryo concerned. In cases where the embryo is straight and the plumule and radicle lie in the same axis as the embryo, remote-tubular germination occurs. When the whole embryo is curved, germination is of the adjacent-ligular type, while remote-ligular germination takes place when the embryo is straight, but where the plumule and radicle lie obliquely to its longitudinal axis.

This general correlation for palms is true also in the case of *J. caffra* and its embryo is straight with the radicle and plumule lying in the same axis as the embryo.

The findings of this study in respect of the depth to which the apocole enters the soil, are contrary to those published by Barry (1957) who states that the hypocotyl descends to 18 inches (450 mm). It is clear from Fig. 9 that the apocole reaches a maximum length of approximately 70 mm.

Germination in other cocosoid palms varies extensively. In *Butia* (Boyd, 1932, *Elaeis* (Hussey, 1958) and *Cocos* (Corner, 1966) germination is adjacent-ligular. *Arecastrum* on the other hand exhibits remote-tubular germination (Gatin, 1906), while germination of *Jubaea* is remote-ligular (Gatin, 1906; Tomlinson, 1960a).

In view of the statements by Boyd (1932) and Moore & Uhl (1973), that remote germination is more primitive than the adjacent type and that the ligular types are more specialised than tubular germination, it would seem that *J. caffra*, with remote-tubular germination, is one of the more primitive cocosoid palms, while the closely related *Jubaea* is slightly more advanced. The coconut, *Cocos nucifera*, it appears, is somewhat more advanced in this respect than either of these two genera.

Fig. 10.
The first expanded eophyll of a *Jubeopsis* seedling (eo_1).

Fig. 11.
Three expanded, simple eophylls (eo 1–3) and the fourth (eo_4) unexpanded foliage leaf. All are entire, lanceolate leaves.

Fig. 12.
The seventh eophyll—irregularly pinnate (eo_7).

(lr—lateral roots; pr—primary root).

Two scale leaves are formed during germination and this number is always constant in *J. caffra*. It is usual for the number of scale leaves to be constant within any given species (Tomlinson, 1960b). However, the number varies from species to species, e.g. one each in *Livistona humilis* and *Phoenix roebelenii* and two in *Phoenicophorium borsigianum* (Moore & Uyl, 1973).

As far as the true foliage leaves are concerned, there exists a gradual transition from the first eophyll to the adult foliage leaf in palms generally (Corner, 1966). Tomlinson (1960a) has devised a classification system of six developmental patterns for the foliage of palms in respect of this transition from juvenile foliage to the adult leaf. The longest series of different eophyll forms as exhibited by *Roystonea* and *Stevensonia* represents the most primitive condition and includes entire, bifidous and pinnate juvenile forms.

The transitional series in the cocosoid palms while having a number of entire eophylls, which indicates a degree of primitiveness, also includes a number of more specialised irregularly pinnate transitional leaves. According to Tomlinson (1960a) this is indicative of a special evolutionary trend and consequently he considers the cocosoid palms as being anomolous in this respect.

Although it has been possible to observe the development of only the first seven eophylls of *J. caffra* during this study, it appears that *J. caffra* is similar to the other cocosoid palms in this connection.

When the radicle tip emerges from the germination pore, it is covered by a protective cap. Gatin (1906) states that the radicles of all palm embryos are protected in this manner and that the cap is in fact a radicular sheath originating from the cotyledonary tissue. This view is supported by Tomlinson (1960a). Von Guttenberg (1960) however rejects this interpretation and describes the cap as being nothing other than a primary root cap, originating from cell tiers in the proembryo which are totally different to the tiers which give rise to the cotyledon.

The results of this study, as well as those obtained from an earlier study of the embryogeny of *J. caffra* (Robertson, 1976) support this latter view and it is thus concluded that the radicular cap found in *J. caffra* is not of cotyledonary origin but that it is in fact a true calyptra originating from tier n′ in the fourth cell generation of the proembryo.

Gatin's (1906) division of germination into two phases, viz. a preparatory phase and a germinative phase is based primarily on the time at which the radicle emerges from the cotyledonary sheath. However, as discussed above, it appears that the radicle is not enveloped by the cotyledonary sheath and consequently the first organ to emerge from the germination pore is in fact the radicle with its rootcap. In view of this, it seems that in *J. caffra* germination consists of a germinative phase only.

In respect of lateral root formation in the seedling, it would seem that the condition found in *J. caffra* is different to that described by Gatin (1906) for other palms. Gatin states that where thick lateral roots are formed, only one is formed at a time and that it takes over the function of the primary root. In *J. caffra* though, three thick lateral roots are formed simultaneously. Furthermore, the primary root is still functional two years after germination, so that it is in fact not immediately replaced by the thick lateral roots.

ACKNOWLEDGEMENTS

The writer is indebted to the University of Port Elizabeth and the C.S.I.R. for their financial support of this project.

REFERENCES

BARRY, D., JR., 1957. The African relative of the Chilean Wine Palm. *Principes* **2:** 180–2.

BOYD, LUCY, 1932. Monocotyledonous seedlings: Morphological studies in the post-seminal development of the embryo. *Trans. Proc. bot. Soc. Edinb.* **31:** 1–224.

BURTT, B. L., 1972. Plumular protection and some related aspects of seedling behaviour. *Trans. Proc. bot. Soc. Edinb.* **41:** 393–400.

CORNER, E. J. H., 1966. *The natural history of palms.* London: Weidenfeld and Nicholson.

GATIN, C. L., 1906. Rescherches anatomiques et chimiques sur la Germination des Palmiers. *Annls. Sci. Nat.* **3/4:** 191–310.

HILL, A. W., 1937. The method of germination of seeds enclosed in a stony endocarp. II. *Ann. Bot.* **1:** 239–256.

HUSSEY, G., 1958. An analysis of the factors controlling the germination of the seed of the oil palm *Elaeis guineensis* (Jacq.) *Ann. Bot.* **22:** 259–284.

MOORE, H. E., JR. and UHL, NATALIE, 1973. The monocotyledons: Their evolution and comparative biology VI. Palms and the origin and evolution of monocotyledons. *Q. Rev. Biol.* **48:** 414–436.

ROBERTSON, B. L., 1976. Embryology of *Jubaeopsis caffra* Becc.: 3. Endosperm and Embryogeny. *Jl S. Afr. Bot.* **42**(4): 285–299.

ROBERTSON, B. L. and SMALL, J. G. C., 1977. Germination of *Jubaeopsis caffra* seeds. *Principes* **21**(3): 114–122.

ROBERTSON, B. L. and VISAGIE, G. P., 1975. *Jubaeopsis caffra*—An Eastern Cape rarity. *The Eastern Cape Naturalist* **55:** 15–19.

TOMLINSON, P. B., 1960a. Essays on the morphology of palms. I. Germination and the seedling. *Principes* **4:** 56–61.

TOMLINSON, P. B. 1960b. Seedling leaves in palms and their morphological significance. *J. Arnold Arbor.* **41:** 414–428.

TOMLINSON, P. B., 1961. *Anatomy of the monocotyledons.* II. *Palmae.* London: Oxford University Press.

VAN DER SCHIJFF, H. P. and SNYMAN, L., 1970. The morphology and germination of the seed of *Elephantorrhiza elephantina. J. Arnold. Arbor.* **51:** 114–128.

VON GUTTENBERG, H., 1960. *Grundzüge der histogenese höherer pflanzen.* I. *Die angiospermum Handbuch der Pflanzenanatomie.* Band VIII Teil 3. Berlin: Gebrüder Borntraeger.

WICHT, H., 1967. Our indigenous palms. *Afr. wild Life* **21:** 39–51.